II. Some Results of Recent Experiments in Hybridising Tephrosia bistortata and Tephrosia crepuscularia. By James William Tutt, F.E.S.

[Read November 17th, 1897.]

The recent experiments made by Dr. Riding and Mr. Bacot in hybridising the two allied species, *Tephrosia bistortata*, Goeze (crepuscularia, auct.), and *Tephrosia crepuscularia*, Hb. (biundularia, auct.), and the interest caused by the exhibition of the specimens, has led to the expression of a wish that some permanent record of the results exhibited by the various broods should exist.

This is my only excuse for this paper.

It is necessary to define the two species with which the experiments have been made, because it has been suggested that they really form but one species. The first, Tephrosia bistortata, is of an ochreous (often tending to ferruginous and fuscous) ground-colour; it occurs in the British Islands in March and again in July, is widely distributed in Scotland and the southern counties of England, and is found in the greater part of the Palæarctic and Nearctic regions. The second brood of this species differs from the first in being, usually, smaller, of a dead white colour and almost entirely without the ochreous tint of the first brood. The second species, Tephrosia crepuscularia (biundularia), has a white ground-colour; it occurs in the British Islands in May and June, that is, at a period intermediate between the two broods of Tephrosia bistortata, is never double-brooded, is widely distributed in Ireland, and the midland and northern counties of England, overlaps T. bistortata in the southern counties of England—in some cases occurring in the same woods, e.q., near Swansea, Leigh Woods (Bristol), the New Forest, Reading, &c.,—occurs in central Europe, but is not known to occur either in southern or northern Europe, nor beyond European territory.

So far, then, the specific separation of these undoubtedly allied species is insisted upon by many specialists. The points urged by them are: (1) The differences in the

eggs; (2) the differences in the general character and appearance of the imagines; (3) the difference in the shape of the wings, those of T. crepuscularia being much the squarer; (4) the independent life-histories of the two insects; (5) the constant difference in the times of appearance, even when inhabiting the same wood; (6) the fixed double-brooded habit of T. bistortata, the fixed single-brooded habit of T. erepuseularia; (7) the fact that the two insects breed true and always produce their own kind. On the other hand, those who maintain the specific identity of the species, do so on the ground that they are not able to refer with certainty occasional individual specimens to one or the other species. So far as the distinctness of two insects with perfectly independent and distinct life-cycles allows us to constitute them as separate species, these may be so considered.

Both species are subject to melanic variation. Melanic aberrations of *T. bistortata* are exceedingly rare, and almost confined to South Wales; on the other hand, melanic specimens of *T. crepuscularia* are very generally distributed in certain districts, such as Delamere Forest, Yorkshire, Mansfield (Notts), Derby, Swansea district (South Wales), &c. There is no district known where only the melanic form occurs, the typical form being regularly present in all localities in which it is taken. The melanic form of *T. crepuscularia* is known as ab.

delamerensis, B.-White.

### Dr. Riding's Experiments.

ORIGIN OF PARENTS USED FOR PAIRINGS.—By a little judicious artificial treatment during February and March, 1897, Dr. Riding obtained a pretty free emergence of *T. bistortata*, *T. ercpuscularia* and *T.* ab. *delamercusis*. These insects were the parents of the hybrids and were obtained as follows:—

(1) T. bistortata.—These were (a) from eggs laid by a female of the second brood in July, 1896, and captured at Clevedon (Somerset), (b) eggs laid by female (second brood) bred by Mr. Bacot also from Clevedon ova. The imagines emerged between February 17th and March 27th, 1897. These were of the large, well-marked, ochreous, springform, known as ab. abictaria, Haw.

(2) T. ab. delamerensis.—These were the imagines from pupe bred from ova laid by a \$\varphi\$ T. ab. delamerensis, captured in the York district. The eggs hatched May 30th-31st, 1896. Imagines of the typical form appeared with those of the melanic form from this batch of eggs; there were no real intermediates between the two forms; emergence took place between February 26th and April 27th (few came out before March 9th and some as late as April 27th).

(3) T. crcpuscularia.—These were reared from ova of a female from the York district, the ova having hatched June 3rd-4th, 1896. The melanic form appeared w the type in almost equal proportions. The imagines emerged between March 7th and the end of the first week

of April.

Selections from these three broods from which the parents were chosen, together with a brood of *Tephrosia bistortata* that emerged in July, 1897, to show the difference between this second brood and the first brood (*T. ab. abictaria*, Haw.) were exhibited at the meeting of the Ent. Soc. of London, Oct. 6th, 1897. The following are my notes on the specimens exhibited:—(1) *Tephrosia bistortata*.—From Clevedon (Somerset); those exhibited emerged between February 17th and March 8th, 1897. These are of the well-marked southern form, with suffused ochreous ground-colour, distinct basal and subterminal bands, and strongly shaded on either side of the wavy antemarginal line=ab. *abictaria*, Haw. 7 3 and 10 \$\chi\$. The latter more strongly banded and less suffused than the males.

(2) T. bistortata (second brood).—Progeny of specimens of the previously described brood; emerged between June 7th and June 24th, 1897. These exhibit the dead grey colour and ill-developed markings that characterise the second brood of the species, known as ab. consonaria, St. These are especially useful as showing the progeny of T. bistortata, uncrossed by T. crepuscularia.

(3) T. crcpuscularia.—From York ova, bred between March 7th and the end of the first week of April. These are of a rather more suffused form than those from our southern woods; this is probably due to the influence of the melanism that has produced ab. delamcrensis, a form that probably appears as a part of every brood in the York district whence these were obtained. The use of this

rather suffused type form has complicated the colour difficulties in dealing with the hybrids, but has made them

more interesting. 8  $\mathfrak{F}$  and 10  $\mathfrak{P}$ .

(4) T. crepuscularia ab. delamerensis.—From York ova, bred between February 26th and April 27th, 1897. Blackish-grey in colour, deeply suffused but with irregular grey patches; the white antemarginal line not particularly strongly marked.

The broods marked 1, 3 and 4 are those from which the

parents of the hybrids were selected.

RECIPROCAL CROSSINGS OBTAINED.—Fertile reciprocal crossings from 1, 3 and 4 broods (above), were obtained as follows:—

1.—*T. bistortata*  $3 \times T$ . ab. *delamerensis* 9.— $\alpha$ . Paired March 11th; ova deposited March 15th; hatched April 26th–27th.

2.—T. ab. delamerensis  $\mathcal{J} \times T$ . bistortata  $\mathfrak{P}$ .—a. Paired March 9th; ova deposited March 14th; hatched April 18th–19th.  $\beta$ . Paired March 9th; ova deposited March 13th–14th; hatched April 18th–19th.

3.—*T. bistortata*  $\mathcal{F} \times T$ . erepuscularia  $\mathcal{F}$ .— $\alpha$  and  $\beta$ . Two pairings on March 17th; ova deposited March 20th–22nd;

hatched April 25th-27th.

4.—T. crepuscularia  $\mathfrak{F} \times T$ . bistortata  $\mathfrak{F}$ .—a. Paired March 7th; ova deposited March 16th; hatched April 21st–22nd. β. Paired March 14th; ova deposited March 20th; hatched April 22nd–23rd.

Reciprocal crossings that failed were: (1) T. ab. delamerensis  $\mathcal{J} \times T$ . bistortata  $\mathcal{J}$ , two pairings—February 28th and March 12th. (2) T. erepuscularia  $\mathcal{J} \times T$ . bistortata  $\mathcal{J}$ , three pairings,—March 7th, March 10th, March 14th.

HYBRIDS.—I. Hybrids between 3 T. bistortata (Clevedon) × \$\varphi\$ T. ab. delamerensis (York).—No. 1 above. One batch of eggs; hatched April 26th–27th; 100 imagines examined; emerged between June 12th–October 22nd, 1897. These may be roughly divided as follows:—

These two females are very small, and would belong to the preceding set, but for the remarkable development (1) of the square spot about two-thirds towards the apex of the forewing and placed between the submarginal and marginal lines; (2) of the transverse bands, which suggest strongly a superficial likeness to T. consonaria, Hb. [See further notes on this form in Bacot's inbred series from Batch VI (p. 32).]

3 3

Bred June 18th, June 21st and June 24th. I am scarcely able to distinguish these from typical T. crepuscularia, they are rather more suffused, and hence tend to approach the set

following,

4 2 15 3

These are remarkable. The ground colour is pale, but with much fuscous suffusion; strongly marked transverse lines, tending to form bands by shading within the basal and outside the median lines. They are totally unlike the southern T. bistortata ab. abietaria (the male parent) and T. bistortata ab. consonaria (the summer broad); superficially the paler ones are not very unlike T. erepuscularia (the York form). On the other hand, they are quite inseparable from Perthshire T. bistortata, which is a very specialised form of the species. They are much larger and broader winged insects than one ever obtains among T. bistortata ab. consonaria.

25 ₹ 32 ♀

Uniformly suffused and practically ab. delamerensis. The males are darker (blackishfuscous) than the females, with stronger transverse lines and a more or less clearly defined subterminal line; the females are uniform, grey-black in colour, with ill-defined markings, and here and there small irregular patches of the typical pale coloration.

2 7 1 9

The forewings approaching ab. delamerensis, the hindwings more or less typical; probably nearer delamerensis than any other form.

2 pupæ remained unemerged on November 10th, 1897.

43

23

13

26 3

12

These are very close to ordinary second brood T. bistortata, but have the ground-colour rather more suffused than is usual in that form.

These are very like small T. erepuscularia,

These are very like small *T. crepuscularia*, the tint and markings are almost identical with the Yorkshire specimens of this species.

These have the size and markings of the last set, but are ochreous, and tend in this respect to come nearer *T. bistortata* ab. abietaria.

Of the same fuscous suffused form as those described in the last crossing as resembling the Perthshire *T. bistortata*.

Larger and almost indistinguishable from the first brood of *T. bistortata*, the forewings rather less ample towards apex.

These are of the ab. delamcrensis, although some are more uniformly grey than the pure bred examples of this aberration. The dark transverse markings are very ill-defined, but the pale subterminal line is perhaps a shade more well-developed than in the specimens of last crossing. The single female of this brood is small, ill-developed, and has crippled wings.

60  $\uparrow$  1  $\uparrow$  | Complete brood; no pupæ going over.

The two crosses just summarised represent the reciprocal crosses of typical Tephrosia bistortata and T. crepuscularia ab. delamerensis. The following points are worthy of notice. I.—Percentage of a form approaching ab. delamerensis in the two crossings: (1) T. bistortata  $\mathfrak{F} \times T$ . ab. delamerensis  $\mathfrak{F} = 60$  per cent. (2) T. ab. delamerensis  $\mathfrak{F} \times T$ . bistortata  $\mathfrak{F} = 40$  per cent. II.—Percentage of females: (1) in 1st crossing = 52 per cent.; (2) In 2nd

crossing = 1.64 per cent. III.—Percentage of the suffused form resembling Scotch *T. bistortata*: (1) In 1st crossing = 19 per cent.; (2) In 2nd crossing 3.3 per cent. IV.—The crossing in which *T. bistortata* was the male parent has produced by far the larger and more vigorous-looking offspring.

III. Hybrids between ♂ T. bistortata (Clevedon) and ♀ T. crepuscularia (York).—No. 3 above. Two batches of eggs; hatched April 25th-27th; larvæ fed up together; 121 imagines examined, emerged between June 17th and November 3rd, 1897. These may be grouped as follows:—

13 429

These are pale specimens, resembling the second brood of *T. bistortata* in their small size, but distinctly of a cleaner white, thus approaching the ground-colour of *T. crepuscularia*, and with the fine median transverse shade or line, between the elbowed and basal lines (observable in the York *T. crepuscularia*, but practically obsolete in the Clevedon *T. bistortata*). They also show a tendency to form, by means of darker shading outside the elbowed line and within the basal line, transverse bands.

61 ₹ 9 ♀

These, the bulk of the specimens, have the ground-colour much suffused with fuscous and the transverse lines and shades distinct, resembling closely the Perthshire *T. bistortata*; the earlier emerged specimens of this form are smaller and lighter, the later larger and darker.

3 3 5 2

These closely resemble small specimens of the early brood of *T. bistortata*, although one sees none like them in nature. They are as strongly marked as the last, but suffused deeply with ochreous instead of fuscous.

65 ₹ 56 ♀

Two emerged October 31st and November 3rd. Complete brood; no pupe going over.

IV. Hybrid between ♂ T. crepuscularia (York) × ♀ T. bistortata (Clevedon).—No. 4 above. Two batches of eggs; hatched April 21st-23rd; larvæ fed up together; 40 imagines examined; emerged between June 16th

and November 1st, 1897. These may be grouped as follows:—

93 - 9

3 7

28 3

These are small dull grey males with the ground-colour much suffused as in the pale males of crossing II. One is inclined to say that they have a slaty hue. The marks are ill-defined, since they merge into the darkish ground-colour. They resemble the second brood of *T. bistortata* in the absence of definite markings and general suffused appearance; they approach *T. crepuscularia* in the squarer forewings. These emerged chiefly in June.

Small; ground-colour strongly suffused with ochreous; transverse markings moderately

distinct.

Rather larger, and fuller winged than the pale specimens. Of the form with the ground-colour suffused with fuscous. These larger, darker and more strongly marked specimens were the last to emerge, chiefly in late September and October; two as late as October 30th and November 1st respectively.

40 ♂ -- ♀

5 pupæ going over on November 10th, 1897.

The two last crosses enumerated represent the reciprocal crosses of typical T. bistortata and T. crepuscularia. The following points are noticeable. I. Cross with T. bistortata as  $\mathcal{F}$  parent produced 47 per cent. females. The cross with T. crepuscularia as  $\mathcal{F}$  parent produced no females. II. In both crossings the earliest specimens to emerge were much the palest. These were females in the first case, males in the second. The ochreous specimens were those that were intermediate in the pupal state; the darkest, largest, most strongly marked and most vigorous-looking were much longer in the pupal stage.

# Mr. Bacot's Experiments.

ORIGIN OF PARENTS USED FOR PAIRINGS.—These were from the same localities as those used by Dr. Riding, viz., Clevedon (Somerset) for T. bistortata and York district for T. crepuscularia.

RECIPROCAL CROSSINGS OBTAINED.—Fertile reciprocal crossings obtained were:-

1.—T. bistortata  $\mathcal{Z} \times T$ . ab. delamerensis  $\mathcal{Z}$ .—Paired

March 9th.

2.—T. ab. delamerensis  $3 \times T$ . bistortata 9.—Three pairings. a. Paired February 26th; ova deposited April 6th. B. Paired March 5th. y. Paired March 9th; ova deposited April 7th.

3.—T. bistortata  $\mathcal{J} \times T$ . crepuscularia  $\mathcal{J}$ .—Two pairings. a. Paired March 9th; hatched April 8th-9th.

B. Paired March 9th; hatched April 8th-9th.

4.—T. crepuscularia  $\mathcal{Z} \times T$ . bistortata  $\mathcal{Q}$ .—Paired Feb

ruary 27th.

Crossings that failed were: (1) T. erepuscularia 3 × T. bistortata \( \mathbb{?} \). Paired February 27th. (2) T. ab. delamerensis  $\beta \times T$ . bistortata  $\mathcal{P}$ . Paired March 4th.

Hybrids between 3 T. bistortata  $\times \ ?$  T. ab. delamerensis. [Ova received from Dr. Riding.]—They are part of Dr. Riding's cross marked I, eggs laid March 15th, hatched April 26th-27th. Examined 21 specimens = 11 males, 10 females.

43 49 The males dead grey, not ochrous, fairly well marked, showing the more definite markings of T. bistortata; the females are almost pure white with the fuscous lines distinct, but the transverse shading usually united with them almost obsolete.

73 6 9

These may be classed as ab. delamerensis although six males only carry the dark groundcolour of this form; one of the males, and two of the females uniform dull grey (-black), weakly developed, almost without markings, and with a tendency to be diaphanous; the remaining four females, saved for eggs, are worn, but were evidently of the same type. This ill-developed form of ab. delamerensis is undoubtedly due to the crossing, the rapid feeding of the larva, and the production of a second brood, a phenomenon never occurring in nature. The other portion of this brood shows the same peculiarities in a rather less marked degree.]

II. Hybrids between 3 T. ab. delamerensis  $\times ?$  T bistortata.—No. 2a above. One batch of eggs hatched April 6th; some larvæ full-fed by May 9th; larvæ mostly like that of the 2 parent (bistortata) only a few having the apex of the \(\lambda\) open like the larva of T. crcpuscularia. Most of the larvæ pupated about the middle of May. Imagines commenced to emerge early in June, at first rapidly and afterwards more slowly until the end of June; there was then a break until July 16th, when they again commenced to emerge and continued to do so at intervals until the first week in September; one specimen emerged during the last week in October. 58 specimens examined all males— 29 pale and 29 dark specimens.

18  $\beta - \varphi$  Of a cold grey colour, near (but whiter than) the normal second broad of T. bistortata, just showing the dull grey suffusion so characteristic of Yorkshire T. crcpuscularia; the transverse markings and shades well developed.

113 - 9

Having the same well-marked characters as the last, but strongly suffused with ochreous.

29 3

The ground-colour of an uniformly cold steely grey, only two showing a suspicion of a warmer brown tone, otherwise uniformly dark like ab. delamerensis; the darker transverse lines and shades obsolete, the whitish subterminal line moderately developed but not conspicuous; irregular grey patches and streaks on all the wings.

58 ? - ? 1 pupa unemerged on November 16th.

This brood is most uniform in size, rather larger than is usual in second-brooded T. bistortata. There is a very strong, albeit almost indefinable, suspicion of both parents in every specimen, due perhaps to the general tendency towards a slight lengthening of the wings, a tendency to ochreous in some, the running of the markings into transverse bands, all characters of T. bistortata; whilst the whiter ground colour, the defined character of the square spots (one at the lower end of the discoidal cell, the other on the submarginal line) tend towards T. crepuscularia, and taking the brood as a whole it distinctly leans towards the latter. Few of these emerged late, but these are the

most ochreous. Comparison with Dr. Riding's parallel (II) cross, many of which were much longer in the pupal stage, is instructive.

III. Hybrids between  $\Im$  T.bistortata  $\times \Im$  T. crepuscularia. —Of this cross there were two different broods. Of the first (a), marked  $\Im$  in Bacot's pairings, the larvæ for the most part followed the  $\Im$  parent (bistortata), only a few have the apex of the  $\bigwedge$  mark open as in the  $\Im$  parent; full-fed from about May 16th-20th. 22 specimens examined—14  $\Im$  and 8  $\Im$ . These emerged in June with the exception of two which came out in July.

143 89

These are an exceedingly uniform batch, the superficial resemblance to second brood *T. bistortata* being very marked. The sexual dimorphism marked; the females whiter, clearer, and less mottled than the males. There is a distinct absence of ochreous and a tendency to the suffusion noticeable in purebred Yorks. *T. crepuscularia*. [None of these emerged late, and none shows any tendency to become dark.]

14 3 8 9

- $\beta$ . (§ T. bistortata ×  $\Im$  T. crepuscularia.)—Of the other brood of this cross (marked  $3\beta$ ), a fair number of the larvæ fed up and pupated very quickly, but others fed up slowly and did not go down until the earliest specimens had commenced to emerge; larvæ unhealthy, a large proportion died. I examined 9 specimens—6 males and 3 females. Four minute specimens— $\frac{15}{16}$ "(§),  $\frac{15}{16}$ "(2 $\Im$ ),  $\frac{15}{8}$ "(1 $\Im$ ). These small specimens emerged in late June, two normal specimens in early July, one on September 29th, and two late in October.
  - These are pale and practically without markings, although faint traces of the various lines can be seen in 1  $\Im$  and 1  $\Im$ ; the second small  $\Im$  with hindwings crippled; these three specimens measure only  $\frac{1}{15}$  in expanse. The other  $\Im$  is also a pigmy, but fuller winged and better marked, being  $1\frac{1}{5}$  in expanse.

7 3 8 2

Normal size of second-brood T. bistortata; ground-colour distinctly ochreous in tint; strongly developed transverse markings. Two of these were October emergences.

Much suffused with fuscous; strongly marked, small, size of second-brood T. bistortata; one emerged July the other September 29th; the only two of Bacot's insects yet examined that approach the Scotch bistortata form.

It may be well to mention here that these tiny specimens are not infrequent in inbred *T. bistortata*. Such a brood as this last is practically useless for comparative purposes.

#### SPECIMENS BRED BY MR. PROUT.

III. Hybrid between & T. bistortata (Clevedon) × ♀ T. crepuscularia (York).—One batch of eggs; 15 imagines examined, emerged from June-August, except one specimen, which emerged September 26th; no pupæ going over the winter.

Pale, differing but little from summer T. bistortata except that the females are poorly marked, the transverse bands being ill-developed.

Pale, with the square spot (noted in Batch I of Dr. Riding's crosses, and Batch VI a and B of Mr. Bacot's) well developed; females paler than males.

Suffused with the ochreous tint of T. bistortata early brood; more strongly marked. These were the last to emerge, two in August, and one on September 26th. The last is the most strongly marked specimen of the brood.

# DR. RIDING'S EXPERIMENTS (Continued).

Complete brood; no pupæ going over.

Besides obtaining reciprocal crossings of the parent species, pairings of the hybrids were obtained by Dr. Riding, between June 13th and 26th as follows:—(1) ?

(† T. bistortata  $\times \ ?$  T. ab. delamerensis)  $\times \ ?$  († T. ab. delamerensis)  $\times$   $\circlearrowleft$  (3 T. bistortata  $\times$   $\circlearrowleft$  T. crepuscularia). (4) 3 (3 T. crepuscularia  $\times$   $\circlearrowleft$  T. bistortata)  $\times$  $\mathcal{L}$  (3 T. bistortata  $\times \mathcal{L}$  T. crepuscularia). (5) 3 (3 T. bistortata  $\times \ ?$  T. crepuscularia)  $\times \ ?$  (\$\frac{?}{T}\$. crepuscu $laria \times \mathcal{P}$  T. bistortata). Of these different crosses, twelve pairings in all were obtained, eleven of which gave ova, and yet of these eleven batches only two were fertile, both crosses of 3 (3 T. ab. delamerensis × \$ sis). The progeny resulting from these two batches are summarised later in this paper (vide, V). Later pairings of  $\mathcal{J}$  ( $\mathcal{J}$  T. crepuseularia  $\times$   $\mathcal{L}$  T. bistortata)  $\times$   $\mathcal{L}$  ( $\mathcal{J}$ T. bistortata × \$\Pi\$ T. ercpuscularia) also proved infertile. Dr. Riding, however, obtained four inbred pairings of 3 (3 T. bistortata  $\times$  \( \Pi \) T. crepuscularia  $\times$  \( \Pi \) (3 T.  $bistortata \times \mathcal{P}$  T. crcpuscularia); one of these produced no eggs, another was infertile, the two others were only partially fertile.

V. SECOND GENERATION OF HYBRIDS.— \$\(\frac{\gamma}{\gamma}\) (\(\frac{\gamma}{\gamma}\) ab. delamerensis \times \(\frac{\gamma}{\gamma}\) bistortata \times \(\frac{\gamma}{\gamma}\) ab. delamerensis).—The parents taken from crossings II, and I above respectively. Two batches of eggs, hatched June 27th-30th; 44 imagines examined; emerged between August 21st and November 3rd, 1897. It is almost impossible to classify these. As an approximation the following table is appended.

83	1 2	Most	nearly	appr	roacl	ning	to	T. al	o. de	ela-
		merensis,								
	}	tendency		color	ous	suffu	sion	very	diff	fer-
2.4		ent there					1 '			

2 3 Of a slaty-grey tint, approaching the hue of Boarmia gemmaria.

Not unlike pale second-brood specimens of *T. bistortata*.

Dark fuscous, well-marked, closely resembling *T. bistortata* from Perthshire.

3 3 1 2 Closely resembling typical Yorkshire T.

13

I am obliged to term these "intermediates," as they will not fall into any of the above divisions. They are moderately well-marked and might be looked upon if found in nature as odd aberrations of either species. Needless to say, such forms do not to my knowledge occur in nature.\*

Unclassified. Quite distinct from anything that I have ever seen.

One emergence on November 4th; 14 pupe still left on November 10th, 1897.

VI. Inbred Hybrids.— f (f T. bistortata  $\times \$  T. crepuscularia)  $\times \$  (f T. bistortata  $\times \$  crepuscularia). —From two batches of eggs:—(1) Paired August 10th; ova laid August 12th; hatched during the fourth week of August, some only fertile: (2) Paired August 13th; ova laid August 15th; hatched first week in September. By October 22nd all except 13 larvæ had pupated. The first two imagines emerged on November 4th, fine full-fed larvæ at that date not having gone down. 5 specimens examined, 3 f and 2 f ; emerged between November 4th and 10th.

These are again perfect intermediates between T. bistortata ab. consonaria and T. crepuscularia. The larger size of the  $\mathcal{L}$ , the uniform grey tint, the ill-defined markings all lean to the former, whilst the squarer wings approach the latter.

Of a cleaner and better marked type. Difficult to place, but certainly more nearly approaching *T. crepuscularia*.

3 3 2 2 The brood only just commencing to appear.

This cross is similar to the two which follow, but two months later. They are not so very dissimilar from the first section (12 % 1 %) of Bacot's Batch VI, but very different from the 9 % specially described.

<sup>\*</sup> I use the term "intermediate" simply to include those specimens in which the characters of both parents are more or less defined without any very strong tendency towards either.

# Mr. Bacot's Experiments (Continued).

In addition to the first crosses already summarised, Mr. Bacot obtained the following more or less fertile crossings of the various hybrids reared from the alreadydescribed broods.

(1).  $\mathcal{F}$  ( $\mathcal{F}$  T. ab. delamerensis  $\times \mathcal{F}$  T. bistortata)  $\times \mathcal{F}$  ( $\mathcal{F}$ T. bistortata  $\times \$ ? T. crepuscularia). Two pairings: a. June 10th. B. August 6th.

(2).  $\uparrow$  ( $\uparrow$  T. ab. delamerensis  $\times \ \uparrow$  T. bistortata)  $\times \ \uparrow$ (3 T. bistortata  $\times$  ? T. ab. delamerensis). Two pairings

on June 10th. (Eggs mostly infertile.)
(3).  $\mathcal{F}(\mathcal{F}T. bistortata \times \mathcal{F}T. crepuscularia) \times \mathcal{F}(\mathcal{F}T. bistortata)$ T. bistortata  $\times$  T. ab. delamerensis). Paired June 11th. He further obtained the following inbred pairings.

(4).  $\mathcal{F}$  ( $\mathcal{F}$  T. bistortata  $\times \mathcal{F}$  T. crepuscularia)  $\times \mathcal{F}$  ( $\mathcal{F}$ T. bistortata  $\times \$ ? T. erepuscularia). Four pairings: a. June 10th.  $\beta$ . June 10th.  $\gamma$ . June 14th.  $\delta$ . June 17th. (A large percentage of the eggs infertile.)

(5).  $\mathcal{F}$  (  $\mathcal{F}$  T. bistortata  $\times \mathcal{F}$  T. ab. delamerensis)  $\times \mathcal{F}$ († T. bistortata  $\times \$ ? T. ab. delamerensis). One pairing,

June 13th.

The following pairings of a hybrid with one of the parent species were also obtained:

(6).  $\mathcal{F}$  ( $\mathcal{F}$  T. ab. delamerensis  $\times \mathcal{F}$  T. bistortata)  $\times \mathcal{F}$ T. bistortata (second brood). Paired June 15th. Only one or two ova hatched, remainder infertile.

(7).  $\mathcal{T}$  T. ercpuscularia (second brood)  $\times \mathcal{P}$  (  $\mathcal{T}$  T. bistor-

 $tata \times \mathcal{P}$  T. ab. delamerensis). Paired July 4th.

The following crosses entirely failed:—(1)  $\mathcal{Z}$  ( $\mathcal{Z}$  T. bistortata  $\times \ ? \ T$ . ab. delamerensis)  $\times \ ? \ (\ ? \ T$ . bistortata  $\times$ Q T. ab. delamerensis). Paired June 12th. (2) 3 (3 T. bistortata  $\times \ \$  T. ab. delamerensis $) \times \ \$  (  $\ \$  T. bistortata × \(\mathbb{T}\). T. erepuscularia). Paired June 14th. (3) \(\frac{1}{2}\) T. ab. delamerensis  $\times \ \ ?$  T. bistortata)  $\times \ \ ?$  (? T. bistortata × \$ T. crepuscularia).

VI.—Inbred Hybrids.—a.  $\mathcal{J}(\mathcal{J} T. bistortata \times \mathcal{J})$ T. erepuscularia)  $\times \$  (T. bistortata  $\mathcal{J} \times T$ . erepuscularia 2).—Both parents came from Mr. Bacot's Batch IIIa. The parents are normal for that brood. Pairing took place June 17th, 1897; 22 imagines examined, 12 3 and 10 \( \text{: these emerged between the middle of August and } \) end of October

123 19

The brood from which the parents were selected was remarkably free from any ochreous tint, the two selected as parents for this brood being absolutely without a trace. These 12  $\Im$  and 1  $\Im$  are of the same well-marked type as the parent form; the males, however, ochreous, more suffused in colour, and rather smaller. The later emerging males are darker than those which emerged first. The female is white, with distinct transverse lines and bands, and the shape of the wings is particularly bistortata-like.

99

These bear no resemblance to either parent, nor to either species from which derived. Five of the specimens are of a clear white groundcolour, and five are tinged with ochreous. The former have the base and centre of the wings with only the faintest traces of the transverse markings; these are rather more evident (though still inconspicuous) in the others. mens all agree in having the inner part of the normally pale submarginal line of the foreand hind-wings conspicuously white (as in well marked ab. delamerensis), edged internally with a very dark, blackish-fuscous line, which develops a conspicuous costal blotch and a very distinct, dark, square spot (about a third down from the apex) on the forewing, reaching to the fringe. This gives the specimens a distinct resemblance to  $\mathcal{L}$  T. consonaria, but, in the latter, the square spot is most strikingly developed in the elbowed, and not on the submarginal, line. The same spots are clearly traceable in T. bistortata and T. erepuscularia, but never show up conspicuously as in these specimens. The hindwing is similarly marked with a conspicuous antemarginal band. One is much reminded of the dark band of Acidalia trigeminata, but in that species it is the elbowed, and not the antemarginal, line that is affected.

 $\beta$ . 3 (3 T. bistortata  $\times \$ ? T. crepuscularia)  $\times \$ ? (3) T. bistortata  $\times \$  T. crepuscularia).—Another brood, the male and female parents of which were selected from the same batch as the last (Bacot's Batch, III, a). The parents also were normal for that brood. Eight imagines examined, 4 3 and 4 2; emerged from August until end of October.

Males small, the female larger. As in the 4 1 last brood, a tendency to ochreous. The female well marked. The last two males to emerge more suffused than the two earlier ones; one very late tending to the fuscous (Perth) form. Otherwise not unlike secondbrooded T. bistortata.

Of the same form as the nine females described in the last brood, but with the peculiar band-like appearance less strongly defined.

43 49

3 2

VII. 3 (3 T. bistortata  $\times \$ ? T. ab. delamerensis)  $\times \$ ? (3 T. bistortata  $\times$  2 T. ab. delamcrensis).—The parents of this brood were both taken from Bacot's Batch I. They paired on June 13th, and produced in September only two small, round-winged imagines—1 & (11 in. in expanse) suffused with ochreous-fuscous and with distinct transverse lines;  $1 \ ? (1\frac{1}{4} \text{ in. in expanse})$ , whitish groundcolour, with basal and median bands, and well-developed submarginal lines to forewings, and median and outer bands to hindwings. Both specimens show traces of a fine, black, longitudinal line on median nervure at outer point of discoidal cell, and a small, black costal blotch at upper end of the basal line. [This latter is most marked in two males of T. crepuscularia (second broad) bred by Mr. Bacot.

VIII. HYBRID CROSSED WITH & OF PARENT RACE.—  $\mathcal{T}$ . erepuscularia (second brood)  $\times \mathcal{P}$  (  $\mathcal{T}$ . bistortata  $\times$ ? T. ab. dclamerensis).—The progeny is, therefore, threefourths T. crepuscularia and one-fourth T. bistortata. The female hybrid chosen for this experiment was of the delamerensis form and taken from Bacot's Batch I. Pairing took place on July 4th. Forty-nine imagines resulted and

were examined; 38 3 and 11 \(\mathref{Q}\). These emerged during September and October. Only 2 \(\mathref{Q}\) were present among the first 37 emergences and 9 among the last 12. These consisted of 31 pale and 18 dark specimens.

22 3 2 3

Considerable ochreous suffusion in groundcolour, otherwise these specimens have quite reverted to *T. crepuscularia* and are of normal size for that species. One is darker fuscous and tends rather to the *bistortata* facies,

7 9

Larger (with exception of one specimen) than males of this brood; well marked females of distinct *T. bistortata* type, but with a suspicion of the whiter ground-colour of *T. erc-puscularia*. [The important factor relating to these females is that these specimens were longest in pupa, and show a tendency to be larger, a common sexual difference in *T. bistortata* in nature, but not in *T. crepuscularia*.]

16 ₹ 2 ♀

These are of the T. ab. delamerensis form, and are practically inseparable from those of the  $\varphi$  parent brood, except that they are more mottled with irregular patches of white.

38 ₹ 11 ♀

With the exception of the 7 females separated from the others above, the remainder of this brood are, to all intents and purposes, *T. crepuscularia*. Only one who had made a very special study of these could tell that the latter had been crossed with *T. bistortata*.

This completes my summary of the various broods that I have examined. The comparisons of the different crosses have been made with: (1) Typical T. bistortata of the first and second broods, bred from Clevedon ova; T. crepuscularia, and T. ab. delamerensis bred from York ova by Dr. Riding. (2) Three second-brood examples of T. crepuscularia (parents of York origin) bred by Mr. Bacot (only five individuals of this brood are positively known to have occurred in England). (3) Some 200 wild specimens (or specimens bred from wild parents) of T. bistortata and about 150 of T. crepuscularia and T. ab.

delamerensis from various Scotch, Irish, Welsh and English

localities in my own collection.

I have, as much as possible, neglected the use of the term "intermediate." It appears to me that it is frequently most carelessly used, and, as generally applied, comprises almost anything from a sort of "piebald" mixture, so to speak, of two species, to the general resemblance a hybrid must bear to both parents, according as we study them from the point of view of one or other of the parents. All the hybrids dealt with in this paper are, with here and there an exception, in varying degrees, intermediates, i.e., almost every specimen appeals, in some part of its facies, to a specialist as resembling T. bistortata, whilst the same specimen, in other particulars, strikes one as resembling T. erepuscularia. Even the (approximately) black specimens, which, from their striking coloration, naturally most conceal any approach to T. bistortata, are distinctly modified in general appearance and wing structure, and show a tendency to the more marked sexual differences apparent in wild T. bistortata. There is also another difficulty which the introduction of T. ab. delamerensis has caused. In nature, specimens of this aberration are frequently marked with irregular patches of white on all, or some, of the wings (they are "piebald" so to speak), and this may well result from the crossing of the type form with its aberration, for, occasionally, the hindwings are of the typical, and the forewings of the same specimen of the melanic, form. This "piebald" condition is very marked in some of the hybrids classed as delamerensis, and this increased "piebald" condition may be the result of hybridity, although one hesitates to say it is so. The ground-colour of the ab. delamerensis so-called, which occurs among the hybrids, is of a much more uniform grey (especially in the females), the scales ill-developed, the markings weak or obsolete, and the size small, in almost all individuals that emerged quickly as a second brood. These features are undoubtedly referable to the hybridisation which has brought about rapid maturity, the hybrid larvæ feeding up rapidly as do those of T. bistortata, producing a second brood, a phenomenon practically unknown in nature in T. crepuscularia. may, therefore, be looked upon as the influence of T. bistortata on the hybrids, since the second brood of this species is characterised by small size, ill-developed markings, and weak colour. It has been deemed advisable, however, to classify these specimens as ab. delamerensis.

The conclusions to which these experiments point may

be briefly summarised as follows:-

1. The intercrossing of the two species may result in every possible intermediate stage of fertility, from complete sterility to the production of the full number of fertilised eggs. These extreme results may even happen when dealing with different individuals of the same brood. [Failure, therefore, in a few individual cases must not be taken as proving that any particular cross is infertile. Individual aberration of the genital organs may lead to failure; one of Dr. Riding's failures happened with a pair that remained in copula two days and then had to be forcibly separated; this probably was due to such an aberration.]

2. Certain crossings produced almost entirely male offspring. [These were (a) the cross T. ab. delamerensis  $\mathcal{F} \times T$ . bistortata  $\mathcal{F}$ . Of two broods of this crossing, the larvæ of which were mixed, Dr. Riding obtained 60 males and but 1 ill-developed female. A cross of the same two forms, as male and female parent respectively, by Mr. Bacot produced 58 males and no female. It would have been easy here, had Dr. Riding's one ill-developed female not emerged, to have assumed that this cross would produce only male progeny. (b). The cross in which T. crepuscularia  $\mathcal{F}$  was paired with T. bistortata  $\mathcal{F}$  produced in Dr. Riding's hands 38 males and not a single female. It is worthy of note that these were the only four fertile crosses obtained in which T. crepuscularia was the male parent.]

3. The hybrids are fertile inter se but to a less extent than in the parent stock, i.e., there appears to be a larger proportion of failures. They are also fertile with the parent stock. [The former part of this conclusion has been amply proved by both Dr. Riding and Mr. Bacot. The latter was proved by Mr. Bacot successfully crossing a \$\textstyle{2}\$ T. bistortata \$\times\$ delamerensis with a \$\frac{1}{2}\$ T. crepuscularia. One might have expected that if the males of a hybrid were capable of fertile union with females of either parent species as shown by Standfuss, that a certain percentage of the females should be so, and probably also with each other. The number of specimens at the disposal of Dr. Riding and Mr. Bacot has made their experiments particularly useful, as it allowed for a large

number of failures to take place, and yet ultimately for

success to be obtained.]

4. The direct hereditary influence exerted by the parents is a great one. [In every case in which one of the parents was a T. ab. delamerensis, there was a large percentage of specimens of, or approaching, this form in the progeny, and this in spite of my opinion on other grounds that T. bistortata is the phylogenetically older and predominant species. In no case in which typical T. erepuscularia was used as a parent were any forms approaching delamerensis produced, although the parent was from a brood producing both the typical and melanic forms.]

5. The older species phylogenetically is more dominant in stamping its characters on the progeny. This is probably the same as Standfuss's statement that the phylogenetically older of the parent species is prepotent. My view is abundantly proved by the extent of approximation (leaving out the direct influence of the ab. delamerensis form) towards T. bistortata in almost all the broods. This approximation is more especially striking in the large broods of Dr. Riding, in which delamerensis does not enter as a disturbing influence. If, as is here assumed, and afterwards attempted to be proved, T. bistortata is phylogenetically a much older species than T. crepuscularia, it is evident that the phylogenetically older parent leaves more mark on the offspring. It may be, of course, that T. bistortata is a predominant species, more active in its vital functions, and more ready to respond to environmental influences, although the variation of T. erepuscularia renders the latter scarcely probable. At any rate, the dominating influence of T. bistortata on the progeny is most marked.

6. The sex-condition of the hybrids depends on the predominating influence exerted by one of the parents. [In the reciprocal pairing in which *T. bistortata* is the male parent, a fair share of females is the result; when *T. crepuscularia* is the male parent the females are practically wanting. This suggests also that the male exerts the greater influence in the production of female progeny and

vice versâ.]

7. A recently formed aberration may be prepotent and dominant over the type from which it has but recently sprung. [This conclusion appears somewhat paradoxical in the face of 5, yet it is evident from these crosses that,

whereas T. bistortata is the more dominant of the two species, T. ab. delamerensis is dominant over typical T. crepuscularia. In cases in which ab. delamerensis is used as a parent, the number of individuals of, or approaching to, this form is rarely less than 50 per cent. In all cases where typical T. crepuscularia has been used its influence has been almost extinguished by that of T. This may probably be explained by the fact that at the present time T. ab. delamerensis is in rapid process of specialisation in its colour development, and that this activity is maintained in the crosses; or it may be explained as following the ordinary laws of natural selection, if it be conceded that variation is important to the existence of the species, since it is simply the survival of the fittest locally. This conclusion does not, then, necessarily conflict with the fact that the phylogenetically older form, which has survived as the fitter over large areas for a long period, is more potent].

8. The re-crossing of a hybrid with one of the parent species, produces offspring scarcely differing from the parent species with which the hybrid has been paired. [This conclusion is weak, so far as it is based only on a fairly large brood (49 specimens) bred by Mr. Bacot by pairing a dark & hybrid (3 T. bistortata × T. ab. delamerensis) with a 3 T. crepuscularia (second brood). These are, therefore, three-fourths T. crepuscularia and one-fourth T. bistortata; the connexion of the latter species is only evident in a tendency to ochreous in the ground-colour of the males, although the latest emergences (7) of the females show very distinctly the T. bistortata cross. With the exception of the slight change in ground-colour, all the other specimens are practically indistinguishable from

typical T. crepuscularia.

9. The inbreeding of the hybrids of the same cross with each other produces a large percentage of individuals differing much from either parent form. [The form frequently produced by this cross has already been described and compared with female *T. consonaria*, which it superficially resembles in some respects. The same form, but of a rather less pronounced type, occurs occasionally in first crosses.]

10. The crossing of the hybrids obtained from original reciprocal crosses tends to produce a mixed progeny, some referable to known forms of the crossed species, others

quite unlike anything ever obtained in nature. [This is very evident in Dr. Riding's double brood of & hybr. delamerensis-bistortata  $\times \$  hybr. bistortata-delamerensis. I consider this and Mr. Bacot's inbred hybrids in many ways the most important crosses of all, for they prove absolutely that the species operated on are really distinct. If, as has been stated, these were simply two racial forms of the same species, with independent life-histories, existing side by side in the same districts, these crosses should have produced one or other of the parent form (or the parent form if both are identical). The production of forms quite unknown in nature by crossing would be quite inexplicable if the species were in any way identical. These experiments support Eimer's view that sexual combination can lead to the production of new forms. I doubt, however, very much whether they could be perpetuated without selection, and should such a cross occur in nature, it would in my opinion (ante, p. 38, par. 8) revert at once if crossed with one of the parent species, and isolation and selection would both have to be carried out for the perpetuation of the new form.]

11. The darkest, best-marked, largest and most vigorous specimens are those which remain longest in the pupal state. [The fact of the females being normally paler than the males in both parent species, suggests that they have less energy (and material) at disposal for pigment-formation than have the males, more energy being required for the formation of the ova. small and of a very pale form, the females are the first to emerge (see Riding, Batch II.), the males following on quickly; on the other hand, when they are larger, darker, and more vigorous, they emerge after the males (vide Bacot, Batch VIII.). As a rule, it may be taken that the size, vigour, and depth of colour are almost directly proportional to the length of pupal life. The gradation in colour (apart from ab. delamerensis) in some of the broods is most remarkable. The very late emerging specimens in Dr. Riding's Batches III. and IV., have resulted in the production of specimens quite different in hue from the colours reached by the parent species, either at Clevedon

or York.]

12. The hybrids have lost all regularity as to the time of emergence, *i.e.*, hybridity causes continuous-broodedness. [All the crosses result in producing progeny which

pair and in turn produce progeny, and so on ad. inf. Even the T. crepuscularia, one of the most regularly single-brooded species in England (only five undoubted second-brood specimens are known) are unable to prevent this. Broods of almost all the crosses are now feeding, and in one case, at least, larvæ of hybrids of the third generation. Allowance must of course be made for the tendency of the prepotent T. bistortata to be doublebrooded (and that it will occasionally also produce an individual or so of a third brood), but these broods emerge almost entirely and appear capable of going on indefinitely if food be provided. The same tendency is observable in hybrid Smerinthus populi-ocellatus, both parents of which are normally single-brooded species, but the hybrids from which always emerge in autumn as a second broad (vide Ent. Record, I, pp. 202-203, where Kirk gives:—Pairing May 31st, 1890; larvæ pupated July 20-27th; imagines bred after being in pupa three weeks; normal S. ocellatus and S. populi fed up side by side going over the winter). It is also observable in hybrid Amphidasys strataria-betularia, both of which parents are absolutely single-brooded (vide Ent. Record, II, p. 83, where Dr. Chapman records a  $\mathcal{F}$  A. strataria paired with a  $\mathcal{F}$  A. betularia ab. doubledayaria; fertile eggs produced; larvæ fed up on sallow and oak; half-a-dozen larvæ missed a moult and pupated early; emerged some time during winter (as they were found dead in spring).]

The following general observations have also been noted

in my examination of the insects:-

The influence of the male parent is less than that of the female, as shown by the percentages of T. ab. delamerensis, but this varies with individual broods.

When T. bistortata is the male parent, the progeny is more vigorous than when T. crepuscularia is the male

parent.

The greater vigour of the male results largely in the production of female offspring. When the male is of the dominant species, females are developed in fair proportion; when the female is of the predominant species, males are largely in excess.

The hybrid facies of all the first crosses, and the ease (judged from the one large broad at disposal) with which the progeny of first crosses revert to one or other of the parent forms, when crossed therewith (even when

that form is the younger phylogenetically and therefore less prepotent), suggests very strongly that the insects under consideration are true and distinct species. It also shows that if accidental hybridisation took place in nature, the progeny of the hybrids thus produced would, if such hybrids paired with either parent species, lose its separate identity and merge at once into that parent species with which it crossed. Although possible, it appears very improbable that any lepidopterous hybrids would in nature continue their race apart, and this, not from any want of vigour, but from want of sufficient isolation. Given the latter, then it is quite possible that they should do so. It must not be overlooked that the continuous-brooded element introduced into their habits would also tend to their destruction, as the eggs laid during October and November would hatch and the larvæ perish from want of food.

The tendency for all the late-emerging specimens to be entirely different from either (1) the Clevedon spring form of T. bistortata (=ab. abictaria, Haw.), (2) the Clevedon summer form of T. bistortata (= ab. consonaria, St.), (3) the typical Yorkshire form of T. crepuscularia, or (4) the T. ab. delamerensis, and to develop a form identical with the Perthshire T. bistortata, a form that does not occur in England, but which closely resembles that found on the Continent, in certain Asiatic portions of the Palæarctic region, and in the Nearctic region, suggests most strongly that the Perth form is, so far as the forms occurring in Britain are concerned, the natural type form of the species. This vast distribution of T. bistortata, when compared with the restricted range of T. erepuscularia (so far as it is known), strongly supports the view that T. bistortata is the older species phylogenetically.

As bearing out No. 12 of my conclusions, Dr. Riding remarks: "The fact of all the insects taking after Tephrosia bistortata in habits, i.e., in a second and even third (second generation of hybrids) emergence in the same year, is remarkable. Virtually, none takes after T. crepuscularia and T. ab. delamerensis in this respect. The environment and captivity cannot have anything to do with causation, as I have pupæ of both these latter and of Perth T. bistortata—bred more or less about the same time and under the same conditions—all going over the winter as pupæ."

Dr Riding further adds: "It may be well to note the

similarity of the single specimen of T. bistortata that is exhibited and that emerged as the representative of a third brood on August 17th, 1896, to a small T. crepuscularia, though the rest of the pupe of the broad that went over the winter emerged as typical T. bistortata in 1897."

Mr. Bacot has given me the following interesting

information on the early stages:—

(1) The ova of T. bistortata are considerably larger than those of T. crepuscularia. The ova of all the hybrids examined approach more nearly in size to those of T. crepuscularia, in some cases being somewhat smaller. Dr. Riding gives the relative sizes of the ova as—T. bistortata (1st brood): T. bistortata (2nd brood); T. crepuscularia: ovum of hybrids :: 4.25 : 3.75 : 3.5 : 3.

(2) The hybrid larvæ feed up more rapidly than those

of either parent species.

(3) There is a slight tendency for the hybrid larvæ to follow the larval form of the female parent; at the same time, there is a much more strongly marked tendency for the larvæ of all the crosses to follow the larva of T. bistortata, i.e., that whilst the larve of all the crosses are very close to those of T. bistortata, as regards the dark united  $\wedge$ , a larger proportion of the cross  $\mathcal{L}$ , crepuscularia × 3 T. bistortata tends to have a distinct gap at the apex than is the case with the reciprocal cross.

(4) In the batches of inbred hybrid crosses that produced fertile eggs, a certain number failed to hatch, an event quite without parallel in the eggs of the first crosses. [Dr. Riding also notes that in the inbred hybrid crossings that he obtained, which produced fertile eggs, only some

were fertile.]

(5) The larva of the inbred hybrids inclined rather to those of T. crepuscularia than to T. bistortata, although a few larvæ had the  $\wedge$  mark united as in the larva of T.

bistortata.